LIFE HISTORIES OF THE MOLLUSCA.

BY A. S. PACKARD, JR.

I. LAMELLIBRANCHS.

HAVING gone thus far along the track leading from the moners to man, we come to where the road branches in several directions. The path from the Protozoa to the sponges, from the sponges to the polypes, and from the polypes to the Ctenophoræ, and through them to the Echinoderms, though at times devious and readily lost, yet in the retrospect is more easily followed than those lying before us. In fact there is no single track leading directly from the lowest to the highest animals. We have to follow distinct lines of development, and, after toiling up one ascent, find that it ends abruptly, without bringing us very near the goal. We then have to retrace our steps, return to the old fork in the road and essay a new path. For example, following up the line of mollusca, we come to the cuttlefishes with their well developed eyes and circulatory apparatus, nearly as complicated as those of fishes. If we follow the ascidian line of development, we trace immediately in their larval condition a *chorda dorsalis* and a relation of rudimentary organs which bear a striking analogy to those of Amphioxus, the lowest vertebrate. Again, in studying the Brachiopods, we follow a line of life which leads us to forms such as the Lingula which combines Annelid characters with remarkable features of its own. If after traversing these paths we take up the long and devious route which leads from the Rotifers through the non-segmented worms up to the leeches and Annelides, to the Crustacea and Insects, we shall then reach animals which in many respects are only inferior to the vertebrates, and in complexity of organization, in their morphology and in their psychological endowments, are on the whole, superior to any other invertebrates.

What is this initial point from which these lines diverge? It is a larval form having a bilateral, cylindrical body, sometimes annulated, divided into a preoral and postoral region, *i. e.*, a head and hind body, with a ciliated crown, often a whip-lash or tuft of bristles, with a mouth, a usually curved alimentary cavity, and anus opening often near the mouth. This stage is seen in the

young Echinoderm, such as the Auricularia or Bipinnaria; or in the Veliger state of the young mollusk; in the young worm, whether the "Actinotrocha" of the Sipunculus, or "Tornaria" of Balanoglossus, or "Mesotrocha" of a higher annelid, or even in the young Rotifers. For such a form the term *Cephalula* may be proposed in allusion to the fact that a cephalic region is indicated in this state, the Gastrula being a simple sac with the head end not differentiated from the opposite extremity. Let the reader compare the gastrula of the sponge (Fig. 49) with the Cephalula of the Trochus (Fig. 138, B) and he will detect the difference between the two stages. This stage is thus named simply to give emphasis to the fact that it is a form common at one stage in their life-history to several entirely different classes of animals, radiate, articulate and molluscan, independently of any theoretical considerations. I will only say that the Cephalula bears an analogous relation to these classes, as the Planula to the Radiates, the Nauplius to the Crustaceans, or the Leptus to the Insects.

We shall see in our future studies of the life-histories of the different classes of invertebrate animals, how often this Cephalula, with its ciliated crown, recurs.

No one has ever given a thoroughly satisfactory definition of the type of Mollusca, and we shall certainly not attempt one here. It may be said, however, that they are in their early stages, and in nearly all (except the Gastropoda, in which the visceral or abdominal end is asymmetrical), in adult life bisymmetrical animals bearing usually an external or internal shell (sometimes the shell is larval and deciduous), with the under lip converted into an organ of locomotion, the large fleshy foot. The nervous system consists of three pairs of ganglia usually surrounding the œsophagus, sending nerve-threads in irregular directions to the different organs.

The Mollusca usually have a well developed heart, more so than in the Crustacea and Insects, situated dorsally and consisting usually of a ventricle and two auricles. The respiratory organs depend or project from the mantle or tegument, and are permeated by a net-work of blood-vessels. A large number have an "odontophore" or "lingual ribbon, a band of teeth rolled up in the mouth. The mollusks are neither radiate nor segmented as in the Articulates or Vertebrates, though certain larvæ are indistinctly annulate as in that of Chiton.

For a further discussion of the characters of the mollusks as compared with the worms the reader is referred to Prof. Morse's memoir "On the Systematic Position of the Brachiopoda."[1]

The following tabular view of the mollusks is copied from Gegenbaur's "Principles of Comparative Anatomy." For further information the reader is referred to Woodward's "Manual of the Mollusca."

MOLLUSCA.

I. LAMELLIBRANCHIATA.
  1. *Asiphonia* (Ostræa, Anomia, Pecten, Mytilus, Arca, Unio).
  2. *Siphoniata* (Chama, Cardium, Cyclas, Venus, Tellina, Mactra, Solen, Pholas, Teredo).

II. CEPHALOPHORA.
  1. *Scaphopoda* (Dentalium).
  2. *Pteropoda.*
    Thecosomata (Hyalea, Cleodora, Chreseis, Cymbulea, Tiedemannia).
    Gymnosomata (Pneumodermon, Clio).
  3. *Gastropoda.*
    Heteropoda (Atlanta, Carinaria).
    Opisthobranchiata (Bulla, Aplysia, Doris, Glaucus, Æolis).
    Prosobranchiata.
      Cyclobranchiata (Patella, Chiton).
      Ctenobranchiata (Paludina, Neritina, Buccinum, Purpura, Murex, Fusus, Conus, Oliva, Strombus, Haliotis).
  4. *Pulmonata* (Lymnæus, Physa, Planorbis, Helix, Bulimus, Limax).

III. CEPHALOPODA.
  1. *Tetrabranchiata* (Nautilus).
  2. *Dibranchiata.*
    Decapoda (Spirula, Sepia, Loligo).
    Octopoda (Octopus, Argonauta).

Development of the Lamellibranchs. It is only within a comparatively few years that we have learned anything of the mode of growth of our commonest bivalve mollusks. To this day the life history of the common clam or quahaug is a mystery. The early stages of the oyster are only partially known. We know much less about the early stages of the common sea mussel; while the history of the fresh-water mussel (Unio) sketched roughly in 1831 by Carus, is still fragmentary. For the first definite knowledge of the metamorphoses of the Lamellibranchs, we are indebted to the distinguished Swedish observer Lovén, who gave between the years 1844 and 1849, a series of sketches more or less complete of

[1] Proceedings of the Boston Society of Natural History, Vol. xv, 1873, 8vo. pp. 60.

a number of marine forms. To him and to Sars, the famous Norwegian zoologist, who made the first sketch of the metamorphoses of the Gastropods, we are indebted for our earliest and most valuable facts in the life-history of the mollusks. Before this, some larval mollusks were regarded as infusoria by Ehrenberg.

Of the mode of development of the oyster, the lowest lamellibranch, the first information was supplied by Lacaze-Duthiers (1854–5), supplemented by the recent (1874) observations of Salensky. While some lamellibranchs, such as the Unio, are bisexual, the oyster is hermaphroditic. The eggs, which are yellow, after leaving the ovary are retained among the gills. A single oyster may lay 2,000,000 eggs. The spawning time of the oyster in Europe is from June to September. During their development the eggs are enclosed in a creamy slime, growing darker as the "sprat" (the term applied to the young oysters) develops.

The course of development is thus: after the segmentation of the yolk (morula stage), the embryo divides into a clear peripheral layer (ectoderm), and an opaque inner layer containing the yolk and representing the inner germinal layer (endoderm). A few filaments or large cilia arise on what is to form the velum or the future head. The shell then begins to appear at what is destined to be the posterior end of the germ, and before the digestive cavity arises. At this stage the two-layered germ is said by Salensky to represent the planula of the sponge. The digestive cavity is next formed (gastrula stage), and the anus appears just behind the mouth, the alimentary canal being bent at right angles. Meanwhile the shell has grown enough to cover half the embryo, which is now in the "Veliger" stage, the "velum" being composed of two ciliated lobes in front of the mouth-opening, and comparable with that of the gastropod larvæ. The young oyster, as figured by Salensky, is directly comparable with the Veliger of the Cardium (Fig. 121).

We have, then, three stages of growth in the oyster, (1) the morula, (2) the gastrula (with the digestive cavity as yet undeveloped and, (3) the veliger with an alimentary canal and a head and hind body (cephalula). This is an epitome of the mode of development of most of the lamellibranchiate mollusks whose embryology is known. Soon the shell covers the entire larva, only the ciliated velum projecting out of an anterior end from between the shells. In this stage the larval oyster leaves the mother and

swims around in the water, the cilia of the velum keeping up a lively rotary motion. In this state Lacaze-Duthiers observed it for forty-three days, without any striking change in form, except that the velum increased in size, and the auditory vesicle appeared, containing several otoliths, which kept up a rapid motion. But still the gills and heart were wanting. Of its further history we know but little, except that it becomes fastened to some rock and is incapable of motion. The oyster is said by the appearance of its shell, to be three years in attaining its full growth, but this statement needs confirmation.

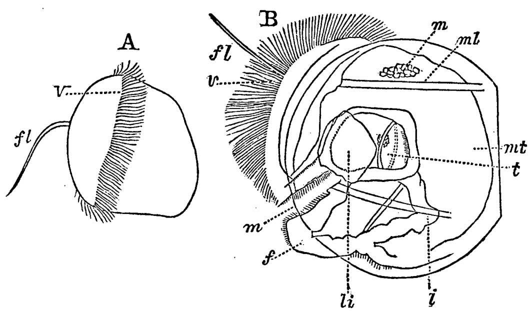
The most complete life history of a bivalve mollusk is that of Cardium (*C. pygmæum*), the cockle shell, as described by Lovén. The egg of this shell is spherical, the yolk being surrounded by a layer of white protoplasm, much as in the eggs of vertebrates. The process of fertilization was observed by Lovén, who saw the spermatic particles of the usual form, *i.e.* with a head and long tail, to the number of a dozen penetrating through the envelopes of the egg out toward the yolk. Following the morula condition the embryo consists of two layers, an outer peripheral clear mass like the "white" of an egg (ectoderm), and a central dark mass, regarded by later observers as equivalent to the inner germinal layer. The embryo now becomes ciliated on its upper surface and already rotates in the shell. On one side of the oval embryo is an opening or fissure,[1] on the edges of which arise two tubercles which eventually become the two "sails" of the velum. This probably represents the gastrula stage, and the embryo already shows a tendency to become bilateral. The next step is the differentiation of the body into head and hind body, *i.e.* an oral (cephalic) and postoral region. Out of the middle of the head grows a single very large cilium, like the whip-lash of the Flagellata, the so-called flagellum (Fig. 121 A, *fl; v*, velum). The shell (Fig. 121 B, *sh*) and mantle (*mt; ml*, muscle) now begin to form. From the inner yolk-mass are developed the stomach, the two liver lobes (*li*) on each side of the stomach (*t*), and the intes-

[1] This primitive opening, the mouth, appears both in Cardium and Crenella, according to Lovén's figures and descriptions, long before the shell begins to form. It is thus not a secondary formation, as Salensky insists, but a primary invagination of the ectoderm. The embryo is therefore properly a gastrula. It will be remembered that in the oyster on the contrary the shell begins to form before the mouth-opening appears. The young oyster at the stage immediately succeeding the morula is, then, a planula; the Cardium and Crenella, a gastrula. This exception does not warrant us in denying a gastrula state to the Lamellibranchs as a class, as Salensky does.

tine (i). The mouth (m), which is richly ciliated, lies behind the velum, the alimentary canal is bent nearly at right angles and the anus opens behind and near the mouth. The velum (Fig. 121, v) really constitutes the upper lip, while a tongue-like projection (Fig. 121, B f) behind the mouth is the under lip, and is destined to form the large impaired "foot," so characteristic of the mollusks.

In a stage previous to this, when the shell only partially covers the animal, the veliger may be compared with the veliger of Trochus (Fig. 138, B) and a remarkable resemblance be traced, the velum, the bent alimentary canal and the foot being almost identical. The shell arises as a cup-shaped organ in both bivalves and univalves, but the hinge and separate valves are indicated very early in the lamellibranchs. The earliest phase of the veliger stage

Fig. 121.



Development of Cardium. After Lovén.

(cephalula) indicated at Fig. 121 A, in which a cephalic and abdominal region is demarked, may be compared with profit by the reader with the embryo infusorian with its cup-shaped body and its crown of cilia, or with the larval Polyzoan or even the larval Brachiopod to be hereafter figured. At the stage represented by Fig. 121, B, the stomach is divided into an anterior and posterior (pyloric) portion. The liver forms on each side of the stomach an oval fold, and communicates by a large opening with its cavity; while the intestine elongates and makes more of a bend. The organ of hearing then arises, and behind it the provisional eyes, each appearing as a vesicle with dark pigment corpuscles arranged around a refractive body. The nerve ganglion (m) appears above the stomach. The two ciliated gill-lobes now appear, and the number of lobes increases gradually to three or

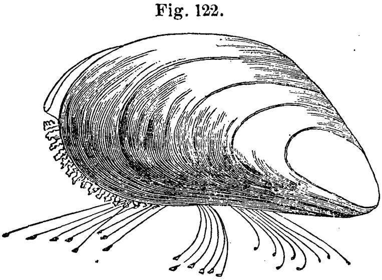
four. The foot grows larger, and the organ of Bojanus, or kidney, becomes visible. The shell now hardens; the mouth advances, the velum is withdrawn from the under side to the anterior end of the shell. In this condition the veliger remains for a long time, its long flagellum still attached, and used in swimming even after the foot has become a creeping organ. Latest of all appears the heart, with the blood-vessels.

Upon throwing off the veliger condition, the velum contracts, splits up and Lovén thinks it becomes reduced to the two pairs of palpi, which are situated on each side of the mouth of the mature lamellibranch. The provisional eyes disappear, and the eyes of the adult arise on the edge of the mantle.

The mode of development of *Crenella marmorata* is nearly identical with that of Cardium. The Crenella is diœcious, the females being known by their reddish ovaries, the males by their white sexual glands. In this genus, however, there is no egg-capsule, and no "white" enveloping the yolk.

All that we know of the development of the common muscle (*Mytilus edulis*, Fig. 122, after Morse) is from studies made by Lacaze-Duthiers on the shores of the Mediterranean. The larval forms were not discovered. The young about $\frac{1}{5}^{mm}$ in length were found swimming at ebb tide on the surface of the water. The shell at this stage is like a Crenella, and there are four long gill lobes, which arise from the outer lamella of the inner gill.

Fig. 122.



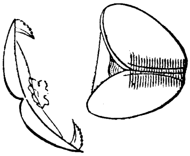
Common Mussel.

The fresh water bivalves pass through entirely different phases of development from the marine forms. The eggs of Cyclas have no shell, no "white" and no yolk skin; they are few in number, from one to six existing in unequal degrees of development in broad cavities filled with a nutritive fluid, and hanging free from the base of the inner gill. The velum is either absent or very slightly developed, and the shell begins to develop at two widely separated initial points on the mantle, according to Leydig.

The fresh water mussels (Unio, Fig. 123, after Morse, and Anodonta) represent another mode of development. In their embryo

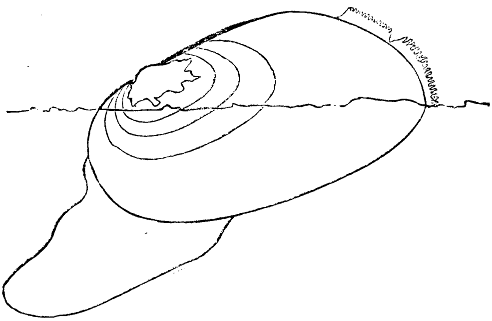
the velum is wanting or exists in a very rudimentary state. The mantle and shell are developed very early. They live within the parent fastened to each other by their byssus. The shell (Fig. 124) differs remarkably from that of the adult, being broader than long, triangular, the apex or outer edge of the shell hooked, while from different points within project a few large, long spines. So different are these young from the parent that they were supposed to be parasites and were described under the name of *Glochidium parasiticum*. They are found in the parent mussel during July and August. The eggs have a shell, "white," and yolk skin and a micropyle. The embryo rotates,

Fig. 124.



Young Unio.

Fig. 123.



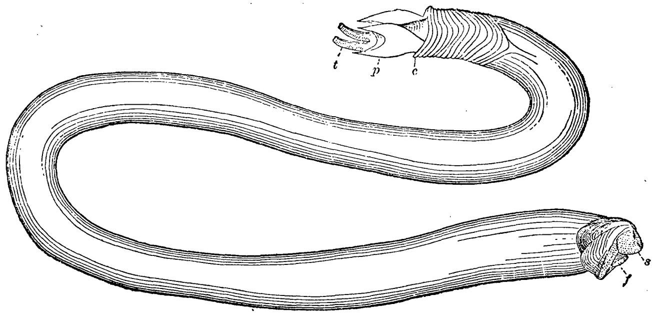
Unio moving through the sand with the siphons expanded.

and remains a month in the egg. When hatched, great numbers still remain among the gills in a mass of slime, and during this time the shell thickens, grows rounder and somewhat longer.

The history of the ship worm (Fig. 125, *Teredo navalis* Linn.) is one of great interest both from a practical and scientific point of view. To the eminent French naturalist, Quatrefages, we are indebted for its life history. Its general development up to the time of the larval stage is much like that of the oyster. The egg has no shell. After fertilization it undergoes total segmentation (Fig. 126, A). The two germinal layers appear as usual, the velum arises much as in the embryo oyster, there being no lash, as in the Cardium, but scattered cilia. Swimming about in this state the embryo would be mistaken for an infusorian. In forty-eight hours after life begins, the cilia begin to disappear and the germ

sinks to the bottom. A deep fissure now separates the germ into halves; meanwhile the mantle and shell have grown, and when

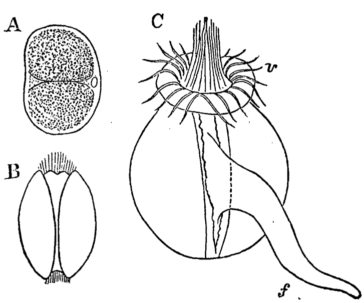
Fig. 125.



The Ship Worm.[1] After Verrill.

five days and a half old the germ appears as in Fig. 126, B, the shell almost covering the larva. Soon after this the velum becomes larger, and then decreases, the gills arise, the auditory sacs develop, the foot grows, though not reaching to the edge of the shell, and the larva can still swim about free in the water. When of the size of a grain of millet, it becomes spherical, as in Fig. 126, C, brown and opaque. The long and slender foot projects far out of the shell, and the velum assumes the form of a swollen ring on which is a double crown of cilia.

Fig. 126.



Development of the Ship Worm.

The ears and eyes develop more, and the animal alternately swims with its velum, or walks by means of the foot. At this stage Quatrefages thinks it seeks the piles of wharves and floating wood in which it bores and completes its metamorphosis. The further changes must be very great before it assumes the adult form of the ship worm with its long body, but these stages have not been observed. Keferstein, however, says that Vrolik saw in July the

[1] Fig. 125, *c*, collar; *p*, pallets; *t*, siphonal tubes; *s*, shell; *f*, foot. After Verrill. Report U. S. Fish Commissioner. Fig. 126, *v*, velum; *f*, foot. After Quatrefages.

larvæ swimming about on the coast of Holland, and some by the middle of the month had bored into the wood and attained the adult Teredo form, though still very small, while others in September still retained their larval, veliger shape. It requires about three weeks for them to complete their metamorphosis. Verrill states that the *Teredo navalis* on the coast of New England "produces its young in May, and probably through the greater part or all of the summer." Quatrefages says that the Teredos die during the winter succeeding their birth.

Keferstein tells us that some lamellibranchs attain their growth in one year. The fresh water mussels (Unio and Anodonta) are thought to live from ten to twelve years, while *Tridacna gigantea* probably lives from sixty years to a century.

The time of spawning usually takes place in summer. The edible mussel (*Mytilus edulis*) and different species of Venus are found with eggs and embryos among the gills from March till May, on the coast of Holland and France, while Pholas and Pandora and most other genera breed from July until September. On the Sicilian coast, according to Poli, Mya and Solen breed early in spring; Pholas, Chama, Venus, Donax, Anomia, Tellina and Mactra in summer; Mytilus edulis from October to December.

We have seen that the Lamellibranchs pass through a true veliger stage, and we shall soon see that their larval forms are directly comparable with the veliger state of most Cephalophora. In after life the "head" of the bivalve, *i.e.* the oral and preoral part of the body, which was fully half as large as the body in the veliger, diminishes greatly in size and importance, becoming finally merged with the postoral region and represented simply by the palpi and foot, the mouth-opening being situated at or near the extremity of the body, so that the old term Acephala well indicates the want of a cephalic region as compared with the large and well developed head of the snails (Cephalophora) and cuttle-fishes (Cephalopoda).

The summary of changes is usually as follows:

1. Egg fertilized by tailed spermatic particles.
2. Morula.
3. Gastrula. (Observed in a very few cases.)
4. Veliger (Cephalula). In Unio and Cyclas wholly or mostly suppressed.
5. Adult Lamellibranch.

LITERATURE.

J. E. Carus. Entwicklung von Unio und Anodonta. (Nova Acta Phys. Med. Leopold. 1831).

S. Lovén. Development of Marine Lamellibranchs. (Ofversigt af Kong. Vetensk. Akad. 1844–1849. Wiegmann's Archiv, 1849. See also Keferstein's abstract in Bronn's Classen und Ordnungen der Thierreichs, vol. iii.)

A. de Quatrefages. Anatomie et Embryologie de la Teredo. (Annales des Sciences Nat. 1848–50.)

Lacaze-Duthiers. Development of various Lamellibranchs. (Annales des Sc. Nat. 1854, 1855).

O. Schmidt. Entwickelung von Cyclas. (Müller's Archiv, 1854).

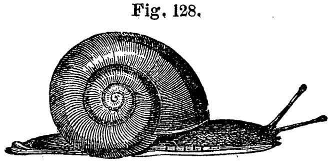
F. Leydig. Cyclas; Anatomie und Entwickelung. (Müller's Archiv, 1855).

W. Salensky. Bemerkungen über Hæckel's Gastræa-Theorie, with three drawings of the embryo oyster and very brief description. (Wiegmann's Archiv, 1874).

II. THE CEPHALOPHORA.

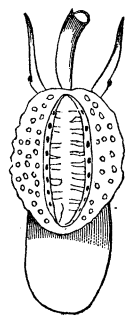
The Cephalophora include not only the Gastropods (snails and whelks) but more aberrant forms such as the swimming Pteropods

Fig. 128.



Helix in its natural position, creeping.

Fig. 127.

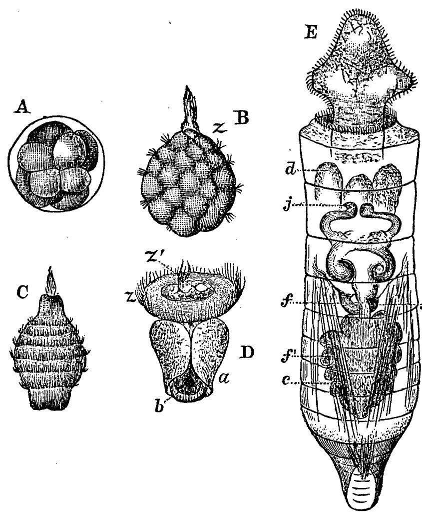


Trivia, a Gastropod. After Stearns.

and the Dentalium, etc. The term indicates the presence in the adult of a well formed head, as distinguished from the acephalous clams. Not only is there a head, but the eyes are restricted to the most anterior part of the preoral region, being, as in the snail, borne on extensile tentacles, whereas in the bivalves, such as the pecten, the eyes are scattered on the edge of the mantle along the entire body. The adult animal is not symmetrical, the mantle containing the viscera being thrown on one side. The foot is greatly enlarged, forming the entire under side of the animal, as in the snail (Fig. 128). The shell is usually external, spiral and asymmetrical, or cup-shaped.

The tooth shell, or Dentalium, is the lowest of its class, and its life history is one of much interest. For the following facts we are indebted to the memoir of Lacaze-Duthiers. The sexes are distinct. It breeds from the beginning of August until the middle of September. After fertilization by the spermatic particles, which Lacaze-Duthiers saw penetrating into the egg, the egg undergoes complete segmentation (A). At the end of this time the embryo swims about by means of tufts of fine cilia (Fig. 129, B), and a pencil of large cilia in front. It then lengthens and is provided with seven bands of cilia, and the larva is remarkably worm-like

Fig. 129.



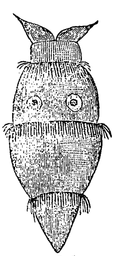
Development of Dentalium.

(C). When two days old the mantle secretes a small shell (*a*) at the end of the body. The ciliated bands now approach and form a swollen ring, or ciliated crown, the velum, as in fig. 129, D, *z*. At this time the shell is median, unpaired and situated on the back of the larva. The lobes of the foot next arise. Fig. 129, E, represents the young Dentalium, after leaving the larval state, and when thirty-five days old. The three-lobed foot protrudes from the shell now enclosing the animal, the rudimentary tentacles (E, *d*) are visible, as well as the subœsophageal nerve-ganglia (E, *j*) and the digestive canal (E, *f*, *f''*) and liver (*f'*). After this, the change into the mature form is slight.

The winged sea-snails (Pteropods) are beautiful creatures found floating on the high seas. With their large, ciliated velum and rudimentary foot they represent the Veliger or larval condition of the Gastropods. There is scarcely a more strikingly beautiful and strange object in nature than the Spirialis with its large heavily ciliated velum, which may be caught in our harbors with the towing net and compared with the young veligerous gastropods often captured in the same net.

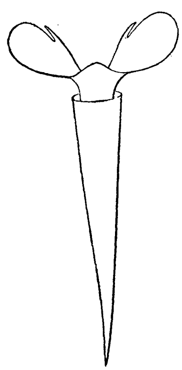
The egg of Cavolinia undergoes total segmentation, and before the large yolk-spheres are absorbed, the spherical embryo swims about like a larval infusorian with a crown of cilia. It may now be called a Trochosphere. Soon the larva assumes a conical form

Fig. 130.



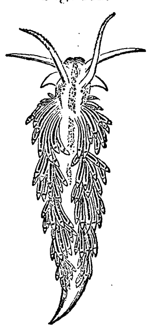
Pteropod larva.

Fig. 131.



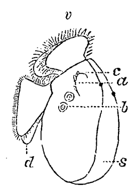
Styliola vitrea.

Fig. 132.



Æolis, a Nudibranch.

Fig. 133.



Larval Nudibranch.

and subsequently the velum greatly expands. Afterwards the Cavolinia, with its projecting foot, assumes a form much like the veliger of Trochus (Fig. 140, B). Fig. 130 (after Gegenbaur), represents a singular Pteropod veliger after the velum has disappeared, consisting of three distinct ciliated segments, like a worm. Fig. 131, after Verrill, represents an adult Pteropod, *Styliola vitrea*, enlarged three times, with the wings of the velum.

Bulla, Æolis and Doris, represent the Opisthobranchiate or naked mollusks, which either, as in the two latter genera, have no shell, with the gills arranged singly or in tufts on the back, or possess a white shell, as in Bulla, the bubble shell. Fig. 132 (from Verrill's Report, represents *Æolis*). Fig. 133[1] (after Schultze),

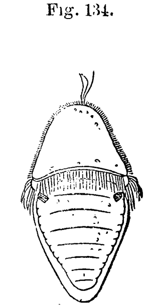
[1] Fig. 133, *d*, foot; *s*, nautilus-like deciduous shell; *v*, velum.

represents the young Tergipes, a naked sea-slug allied to Doris, with its large ciliated velum and foot, the animal being partly surrounded by a large shell (*s*). This shell is finally dropped with the other deciduous larval organs, the gills grow out from the back and the soft elongated body of the adult nudibranch, as this animal is called, is finally attained. It is a singular fact, discovered by Sars, that in the egg-capsules of Dendronotus, as many as six embryos develop side by side.

We will now more carefully study the course of development of a Bulla (*Acera bullata*) as given by Langerhans.

In this animal the yolk of the egg subdivides into two spheres of segmentation, one being much smaller than the other and differing in color. Each of these two cells subdivides into similar halves. The two larger cells then remain passive, while the smaller form a mass of nucleated cells which in two or three days form a layer surrounding the central, inactive yolk cells. On the fifth day arises the first indication of the shell, and on the same day is developed a furrow, the primitive mouth, which separates the cephalic end from the postoral extremity. On the seventh day appear the rudiments of the organ of hearing, and on the day after, the operculum. On the ninth day the pharynx, stomach and intestine begin to develop. On the fifteenth day the otolites are seen in the ear. The liver is next formed, and a few days after the eyes and nerve ganglia, when the larva hatches.

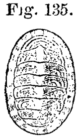
Fig. 134.



Veliger of Chiton.

With the mode of development of Chiton, a cyclobranchiate Gastropod, Lovén has made us acquainted. The larva leaves the egg oval in form, with a ciliated ring in the middle of the body and a long tuft of large cilia on the head. Afterwards it becomes annulated, as in Fig. 134 (after Lovén) and two eye specks appear. Its resemblance to a worm larva is now remarkable. It soon settles down into a quiet life as a Chiton (Fig. 135, *C. ruber*, represents a species found on our shores, from Verrill's Report, after Morse), and the limestone plates correspond to the primitive larval rings.

Fig. 135.



Chiton.

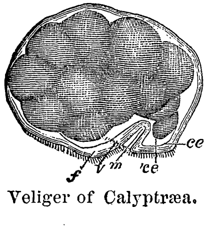
Of the mode of development of the other marine univalve shells (Prosobranchiate Gastropoda), I cannot do better than avail myself of the recent papers of Dr. Salensky. His studies were made

on shells living in the Black Sea, but we have species of Calyptræa and Trochus on our own coast.

Calyptræa sinensis lays its eggs in pear-shaped capsules attached to the same mussel or stone on which it lives. The young of the same brood develop at the same time. Development begins with the total segmentation of the yolk. After it divides into eight cells the blastoderm forms, which consists of a single layer of cells, the result of the subdivision of the first four spheres of segmentation, which grow over and envelop the yolk spheres, thus forming the two germinal layers (ectoderm and endoderm). The cells of the outer layer multiply and form the blastoderm, from which the skin, mantle and external organs, as well as the walls of the mouth arise, while, as in the articulates, the alimentary canal with its dependencies, the liver, etc., arise from the periphery of the yolk cells, the central mass being absorbed.

As soon as the blastoderm is formed, a heap of cells arise and the ectoderm pushes in at a spot which becomes the ventral side of the body. This is the primitive mouth. The anterior part of this cellular heap is the first indication of the "head-vesicle," which becomes a provisional organ well developed in the larva, and is also seen in the embryo fresh-water snails (Pulmonata). The sides of the primitive mouth form the two "sails" of the velum or swimming organ, so characteristic of the larval mollusks, and which was first noticed by Forskal, who wrote on animals just a century ago. Finally, the posterior edge of the infolding, which is also at first a little mass of cells, is the first indication of the foot. The whole surface of the embryo is now covered with cilia, and by their movement the embryo with its fellows, rotates in its capsule.

Fig. 136.



Veliger of Calyptræa.

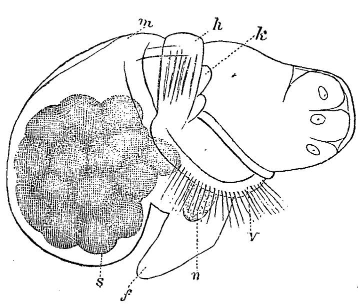
The next change consists in the growth and differentiation of the parts already sketched out. The germ of the foot extends backwards, the mouth-opening deepens and becomes tube-like, the first indication of the pharynx (Vorderdarm). The next most important change is the presence of a layer of cells between the outer and inner germinal layers, which is called the middle germ layer, with cells very unlike the outer layer, from which are developed the muscles of the foot and head as well as the heart

itself. Salensky thinks that this middle layer arises from the outer. It appears first on the ventral side of the embryo. The germ is now of the form indicated by Fig. 136 (*ce*, ectoderm; *'ce*, middle layer, the yolk spheres representing the inner layer, endoderm; *m*, mouth; *v*, velum; *f*, foot. After Salensky).

The next important chapter in the life history of the Calyptræa, is the appearance of the mantle, which arises as a disk-like thickening of the outer germ layer on the back of the embryo. In the middle of the disk the shell grows out as a cup-like cavity which is connected only around the edge with the mantle, but is free in the centre. The ears or auditory vesicles next appear, which, like the eyes, begin as an infolding of the outer germ-layer.

Up to this time the entire body has been symmetrical. Along the longitudinal axis of the body are the foot, the head-vesicle, the germ of the alimentary canal, and on each side a lobe of the velum. The alimentary canal, now further developed, begins to curve to the left, and as the shell grows, the visceral sack, or post-oral portion of the body, hangs over on one side. Not until the organs of sense appeared, the ears with their otolites, and the eyes with their pigment cells, did Salensky discover any trace of a nervous system, and then it was not the cephalic, but the ganglion of the foot which first arises as a mass of nerve cells from the ectoderm.

Fig. 137.

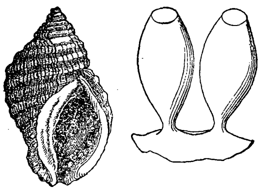


Veliger of Calyptræa farther advanced.

Fig. 137 (after Salensky) represents the asymmetrical larva with the shell enveloping a large part of the body, and the velum (*v*) and foot (*f*) well developed. The larval head forms a third of the whole body and is still finely ciliated. The temporary larval heart (*h*), a large oval vesicle, is situated on the right side of the back of the embryo, between the head and anterior edge of the mantle, in quite a different position from that of the adult heart, which afterwards arises as a new organ. The larval heart contracts rhythmically sixty times a minute. This is an entirely different organ, says Salensky, from the pulsating vesicle or "heart" seen by Duben and Koren in Purpura (Fig. 138, *P. lapillus* and egg capsules, from Verrill's

Report) and Buccinum, or the contractile vesicle found by Semper in Ampullaria, Cypræa, Murex and Ovulum, or the dorsal vesicle of the Pulmonates (snails). There is, however, a similar larval heart in Nassa.

Fig. 138.



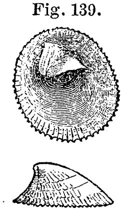
Purpura and Egg Capsules.

At this stage also appears the primitive kidney (Fig. 137, *k*), also a deciduous organ, the permanent, adult kidney arising in another part of the body far behind the larval heart. It resembles the primitive kidneys of the snails (Pulmonates), and appears first as a sort of necklace consisting of four yellowish cells, situated next to the larval heart.

Meanwhile the more the posterior part of the body grows, the larger and more spiral becomes the shell, until the helmet shape of the adult is approached. At this stage also the gill-cavity appears, but there is as yet no trace of the gill itself.

In a succeeding stage the foot has increased in length, the spire of the shell has begun to topple over as it were and fall on one side like a skull cap, and now the adult heart (the pericardium being formed first), and permanent kidney and gills grow out. The gills originate from the ectoderm. It is not until this period that the end of the intestine and anal outlet is formed. The provisional larval organs now begin to disappear, the cephalic-vesicle (larval head) grows smaller, the primitive kidneys disappear. Of the larval visceral organs only the heart remains which, though smaller, still pulsates. It now rests under the mantle in the branchial cavity. There are now two gill-leaves, and finally the permanent heart is formed. The further changes consist in the perfection of all these organs and the development of the shell into the helmet shape of the adult. Fig. 139 (after Morse) represents the common *Calyptræa striata* of our own coast. We have seen that the usual five stages have been undergone, *i.e.* the egg, morula, gastrula (not so well marked as in the pond snail, Fig. 141), veliger and adult.

Fig. 139.



Calyptræa striata.

The metamorphoses of Trochus represent another type of development in the Gastropods, which illustrate points less clearly wrought out in the Calyptræa.

The eggs of *Trochus varius* are very small, spherical, and laid

in masses of jelly on sea weeds. The morula, or mulberry mass, forms as usual. The blastoderm arises from a few small clear spheres of segmentation situated at one pole of four primitive dark morula cells. The four vitelline or primitive cells, instead of remaining passive as in Calyptræa, subdivide, as well as the blastodermic cells. The egg now becomes flattened at one pole and slightly pointed at the other, the latter being the anterior end.

In six hours after development begins, the outer layer begins to form, and the first organ to arise is the velum, which at first consists of a swollen ciliated ring on the anterior end of the embryo. This stage (Fig. 140, A, *v*, velum, after Salensky) is equivalent to the trochosphere (Lankester) of the pond snail. It will thus be seen that the development of Trochus is now very different from that of the Calyptræa, where the velum, head-vesicle and foot arise simultaneously. A little later the mouth and œsophagus arise. Salensky remarks that the Prosobranchiate Gastropods as a rule develop like Trochus. In Vermetus, however, according to the observations of Lacaze-Duthiers, the velum does not arise in the form of a ciliated crown, but as a paired organ. Salensky adds, however, that in other respects there is a strong analogy in Calyptræa to Vermetus and Buccinum and Purpura, which develop like the former mollusk, having a similar larval heart and primitive kidneys, though the mode of development of the external organs is almost wholly unknown. There are thus five genera of Prosobranchiate Gastropods which develop as in Calyptræa, all belonging to the suborder Ctenobranchiata.

On the other hand, *Paludina vivipara*, *Neritina fluviatilis*, and certain Pteropods (*Tiedemannia neapolitana*, *Cavolinia gibbosa*) and a Heteropod (Pterotrachea) are provided, as in Trochus, with a ciliated crown, the first organ lying behind the primitive mouth.

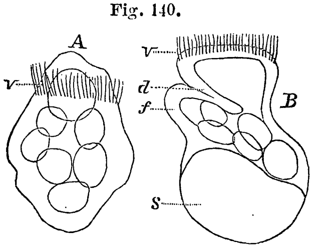
"A good starting point," adds Salensky, whom we have in reality been quoting all along, "for the comparison of the development of Trochus and allied forms, with that of other animals, consists in this stage (Fig. 140, A). A cursory glance at the illustration, will convince one that this condition of the Trochus embryo is similar to the larva of some annelides. Examples of such Annelid larvæ may be seen in some Sabellidæ (*e. g.*, *Dasychone lucullana*) or Spio (*S. fuliginosus*). The latter in escaping from the egg have a more or less oval body consisting of two layers, its only organ

a ciliated crown on the anterior part of the body. The idea of an analogy between the Mollusca and Annelid larva has already been suggested by Gegenbaur. Still more strongly does it follow from these facts, that in the Annelides, as surely as in the Mollusks, the mouth-opening, with the pharynx, arises immediately after the formation of the ciliated crown and somewhat behind the same. Immediately after the formation of the rudimentary pharynx arise the characteristic organs of the two types: in the Annelides the body segments with their appendages; in the Mollusks the foot, shell and two velar lobes."

Salensky then compares the development of Trochus with the Rotifer, Brachionus, and finds some striking analogies. His facts we shall present hereafter in describing from his memoir the life-history of a rotifer.

In the second period of development of Trochus, the true Veliger state is entered upon. The mantle and shell are formed much as in Calyptræa. The body is now flattened, and the ciliated crown projects very slightly. The shell (*s*) has grown considerably.

Fig. 140.



Larval Trochus.

Fig. 140, B, after Salensky, represents this stage. The pharynx (*d*) arises through a tube-like invagination of the outer germ-layer, behind the ciliated crown (*v*). At the same time behind the mouth arises a projection, which indicates the beginning of a foot (*f*). Within the foot, as well as in the anterior part of the body, may be noticed the middle germ-layer, which arises as a layer of cells between the outer and inner germ-layer.

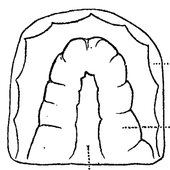
In the following stage the form of the larva is somewhat changed. The shell begins to unroll spirally on the under side of the body. The velum grows more than the middle portion of the head, and the lateral lobes become larger. The operculum also arises on the posterior portion of the foot.

Coming now to the mode of development of the Pulmonate mollusks (fresh-water and land-snails), we find that the aquatic orms undergo a complete metamorphosis, while in the land-snails there is no metamorphosis, and they are hatched in nearly the same form as the adult.

The life history, particularly the earlier stages, of the common pond snail (*Limnæus stagnalis*) of Europe has been worked out with much care by Prof. Ray Lankester, his observations confirming those of Lereboullet, Pouchet and others so far as they extended.

The eggs of Limnæus are deposited in June on the under side of water-plants, in capsules enclosing one, rarely two eggs, and surrounded by a mass of jelly. After segmentation the Gastrula (Fig. 141, *m*, mouth; *ec*, ectoderm; *en*, endoderm) is formed, the primitive digestive cavity or mouth resulting probably from an infolding of the ectoderm. Lankester believes that this orifice or mouth is temporary, the mouth of the adult being a later production. The primitive mouth closes as the embryo enters on the Veliger state, in the earliest stages of which the embryo is oval and surrounded by a ciliated ring, much as in the larval Trochus (Fig. 140, A). This state is called by Lankester the "Trochosphere." A definite Veliger stage is finally attained; the foot is large and bilobed, the mantle and shell then arise and the larva soon passes into the definite molluscan condition, with a shell, creeping foot, mantle-flap and eye-tentacles. The young snail hatches in about twenty days after life begins.

Fig. 141.



Gastrula of the Pond Snail.

Professor Lankester confirms the suggestions already made by Gegenbaur, Morse and Salensky regarding the resemblance of the larval mollusks to young worms. He remarks also that both the Trochosphere and Veliger forms are "well known and characteristic of various groups of Worms and Echinoderms, and the latter is seen in its full development in the adult Rotifera, and in the larval Gasteropoda and Pteropoda. The identity of the velum of larval Gasteropods, with the ciliated disks of Rotifera, seems to admit of little doubt, and it would be well to have one term, *e. g.*, velum, by which to describe both. The Trochosphere is the earlier, more or less spherical form in which the velum is represented by an annular ciliated ridge, and which is sometimes (*e. g.*, *Chiton*) provided with a polar tuft of long cilia.

"The cell, polyblast (morula), gastrula, trochosphere, and veliger phases of molluscan development are not distinctive of the molluscan pedigree; they belong to its præ-molluscan history. The foot, shell-gland, and the odontophore are organs which are

distinctively molluscan—the last characteristic of the higher Mollusca only—the other two of the whole group, and their appearance must be traced to ancestors within the proper stem of the molluscan family tree. The foot is essentially a greatly developed lower lip."

We would add that the Molluscan as well as Annelid Trochosphere may be directly compared (morphologically, not histologically) with the embryo Infusoria (see Fig. 33, E, p. 91) and the ancestry of the Mollusca as well as the Vermes should, as Haeckel declares, be traced back to the Infusoria, perhaps the parent-forms of the entire animal world above the Protozoa.

The usually hermaphrodite Cephalophora, as a rule, to sum up the different phases of their metamorphosis, pass through the following stages:

1. Egg.
2. Morula.
3. Gastrula. (sometimes suppressed?).
4. Veliger (the earliest substage being the Trochosphere, which passes into the generalized Cephalula form; or, restricted to the mollusks, the Veliger stage).
5. Adult mollusk, with foot, shell and often lingual ribbon (odontophore).

LITERATURE.

Sars. Development of Nudibranchs. (Wiegmann's Archiv, 1837, 1840, 1845).

Pouchet. Théorie positive de l'Ovulation spontanée, etc. Paris, 1847.

Leydig. Ueber Paludina vivipara (Siebold and Kölliker's Zeitschrift, 1850).

Koren and *Danielssen.* Bidrag til Pectinibranchiernes Udviklingshistorie. Bergen, 1851, 1856. (Wiegmann's Archiv, 1853).

Kölliker and *Gegenbaur.* Entwickelung von Pneumodermon. (Siebold and Kölliker's Zeitschrift, 1853).

Gegenbaur. Untersuchungen ueber Pteropoden und Heteropoden. Leipzig, 1855.

Claparède. Anatomie und Entwickelungsgeschichte der Neritina fluviatilis. (Müller's Archiv, 1857).

Lacaze-Duthiers. Histoire de l'Organization, du Dévelopment, etc., du Dentales. (Annales des Sciences Nat. 1858).

Lereboullet. Recherches d'Embryologie comparée sur le Dévelopment de la Truite, du Lézard et du Limnée. (Annales des Sciences Nat., 1862).

Salensky. Beitrage zur Entwicklungsgeschichte der Prosobranchien. (Siebold and Kölliker's Zeitschrift, 1872.)

Langerhans. Zur Entwickelung der Gastropoda Opisthobranchiata. (Siebold and Kölliker's Zeitschrift, 1873).

Lankester. Observations on the Development of the Pond Snail. (Quart. Journ. Microscopical Science, 1874.)

Consult also Keferstein, the author of vol. 3 of Bronn's Classen und Ordnungen der Thierreichs; 1862-66; and papers in different journals and transactions of Alder and Hancock, Carus, Krohn, Lacaze-Duthiers, Lovén, Müller, Reid, Schmarda, and Semper.

Development of the Cephalopods. Though the homologies of the Cephalopods with the Cephalophora, particularly the Pteropods, are quite direct, yet the cuttlefishes differ greatly in their mode of growth, particularly in the embryological stages. While the work of Kölliker on the development of the Cephalopods is a classic, yet I shall here avail myself in part of Ussow's more recent work. His observations, made at Naples, are based on two species of Sepia, Sepiola, Loligo and *Argonauta argo*, and they agree so well in their embryology, that the following description answers for all. In the partial segmentation of the yolk, Ussow, as Kölliker before him, was reminded of the same process in the eggs of birds and the turtle. It begins on one side of the yolk; a primitive furrow arising, which is intersected at right angles by a second furrow forming four divisions, afterwards eight, until finally a one-layered germinative disk (blastoderm) is formed on a portion of the surface of the egg, on the second day after development begins. The inner germ-layer then arises, which farther splits into two sub-layers (the outer of which is the dermo-muscular, and the inner the intestino-fibrous).

In Loligo and Sepiola by the 7th or 8th day the germ becomes perfectly spherical and ciliated in portions, so that it rotates in its sac.

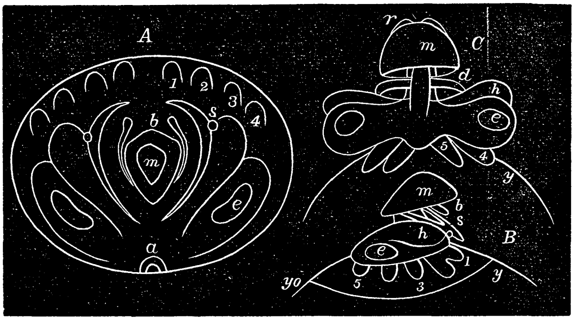
In the second period of development, that of the production of organs, the blastoderm covers the entire yolk. The mantle begins to form, next the rudiments of the eyes arise from the ectoderm, and the mouth appears. The embryo is now like a convex disk, or rather a hollow hemisphere.

On the 10th day the gills, funnel, arms and anal tubercle make their appearance, the germ of the gills arising from the dermo-muscular sub-layer of the middle germ-lamella.

On the 11th day the rudiments of the auditory organs, the pharynx and salivary glands arise, as well as the anal orifice, and on the succeeding day the auricles of the heart, the pericardium arising afterwards. The walls of the aorta and of the larger arteries and veins, with the offshoots of the latter (the so-called kidneys), are developed from the cells of the middle lamella, which become elongated and arrange themselves in rows. On the 13th day the ink-sac develops, and the liver. The intestinal tract originates from the primitive invagination of the outer germ-layer (ectoderm) as in Amphioxus, Ascidia, some Cœlen-

terates, the Brachiopoda, Vermes, etc. As to the mode of origin of the nervous system, Ussow says "I have been compelled to

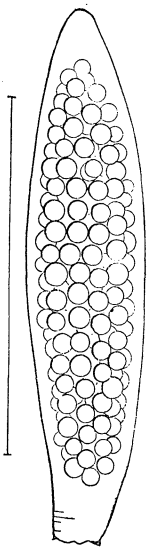
Fig. 142.



Development of the Cuttle Fish.

give up forever the hope of finding any resemblance to its development in the Vertebrata, Tunicata, Annulosa and Mollusca."

Fig. 143.



Egg Capsule of Loligo Pealii.

All the ganglia of the Cephalopoda originate from more or less compact thickenings of the middle germ-lamella (dermo-muscular sub-layer), as in the peripheral ganglia of the vertebrates.

Ussow was unable to trace the origin of the genital glands, as they do not arise until after the animal is three days old, and he could not keep his specimens alive beyond this period.

Now returning to Kölliker's memoir for our information regarding the later stages, Fig. 142, A (*m*, mantle; *b*, branchial processes; *s*, siphonal processes; *a*, mouth; *e*, eyes; 1–5 rudimentary arms, after Kölliker) represents the disk-like embryo resting on the surface of the yolk; B, a side view of the embryo when farther advanced (*y*, yolk sack; *h*, head), and C the same still older, the yolk sac still smaller, the contents having been partially absorbed. Soon after this the body and arms grow longer, and the animal moves about in its shell.

For our information regarding the still later history of our native cuttle fishes we are indebted to the observations of Prof. Verrill, from whose report on the Invertebrates of

Fig. 145.

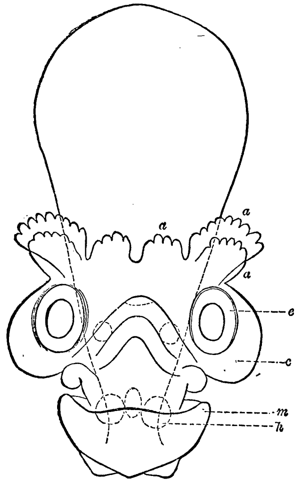


Fig. 144.

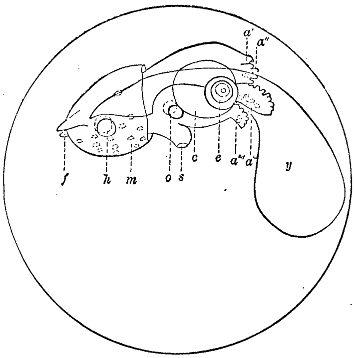


Fig. 146.

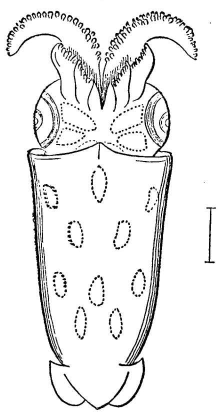
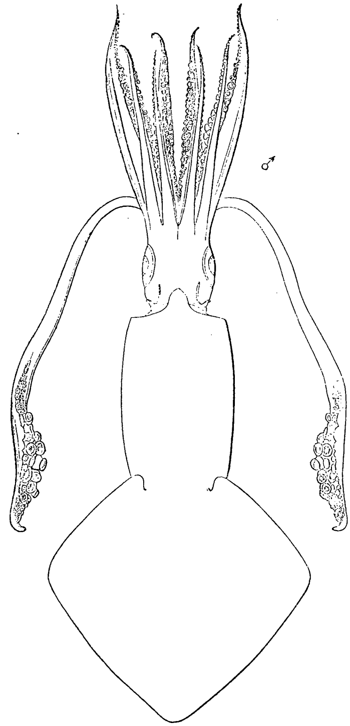


Fig. 147.



Development of a Cuttlefish. After Verrill.

Vineyard Sound in Prof. Baird's U. S. Fish Commission report these cuts are taken. Fig. 143 represents the egg-capsule of *Loligo Pealii.* Fig. 144[1] represents the young of the same cuttle fish, with the yolk sac (*y*). Fig. 145 represents the same farther advanced, while Fig. 146 gives an idea of the same after hatching, the yolk having been completely absorbed. Another species of cuttle fish (*Loligo pallida*) is represented by Fig. 147.

Such is the usual mode of development of the cuttle fishes. But in an unknown form probably over three feet in length, as its mass of eggs was thirty inches long, the mode of development is entirely different. The growth of the embryo is greatly accelerated, and immediately after segmentation it assumes a state analogous to the Trochosphere of other mollusca. To Grenacher's beautiful

Fig. 148.

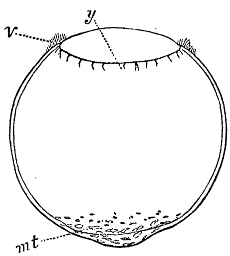
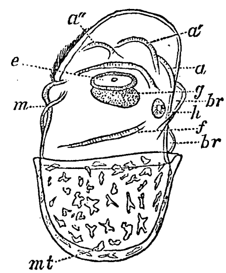


Fig. 149.



Development of an unknown Cuttlefish.

memoir we are indebted for the following facts regarding the life-history of this cuttle fish, whose adult form is unknown. He studied the eggs found floating in the Atlantic ocean, and was unable to raise it to maturity. After partial segmentation, the process being indicated by from five to eight radiating streaks, on the surface of the yolk, the embryo assumed the form indicated by Fig. 148, which represents the blastoderm growing around the under pole of the yolk mass and approaching the anterior end, where there is a swollen, ciliated band (*v*) apparently identical with the velum of the Trochosphere of the lower mollusca. This is an interesting point as Grenacher adopts Lovén's opinion that the arms of the Cephalopods represent and

[1] Fig. 144 *a*, *a''*, *a'''*, *a''''*, the right arms belonging to four pair ; *c*, the side of the head; *e*, the e e; *f*, the caudal fins; *h*, the heart; *m*, the mant in which the color-vesicles are already developed and capable of changing their colors; *o*, th. internal cavity of the same; *s*, siphon. The letters in Fig. 145 a .e the same (after Verrill).

are homologous with the velum of the lower mollusks, particularly the Pteropods, and not with the foot as commonly urged.

This spherical stage is also remarkable for the early appearance of the mantle, with the contractile pigment cells (chromatophores). It will be seen that the entire egg is, as in the lower mollusks, converted directly into the embryo. The embryo soon elongates, the mantle grows, the eyes and arms bud out, and the form of the adult is rapidly sketched out as in Fig. 149 (m, mouth; a, a', a'', arms; f, inner and outer funnel-layer; mt, mantle, the dotted line ending in a chromatophore; h, ear; g, optic ganglion; e, eye.

We thus have in the embryology of this form, which seems not very different from Loligo (as may be seen in a more advanced stage figured by Grenacher not reproduced here), a mode of development much more like the lower mollusks than was before suspected.

Of the embryology of the fossil Tetrabranchiate Cephalopods (the Ammonites, etc.) we know from the beautiful researches of Professor Hyatt that the shell in Ammonites as well as Goniatites begins as a minute globular sac; in Nautilus this sac "is not retained, but traces of its former existence are apparent on the apex of the first whorl, in the form of a scar or cicatrix."

Summarizing the known facts regarding the living, dibranchiate Cephalopods, we have eggs and spermatic particles developed in separate sexes, the egg passing through the following phases.

1. Partial segmentation, analogous to that of Vertebrates.

2, *a*. Trochosphere (?) or germ developing on the surface of the yolk and gradually absorbing it; the Gastrula state suppressed; or, as is more usually the case (*b*), the adult form is directly attained.

LITERATURE.

Kölliker. Entwickelungsgeschichte der Cephalopoden. Zürich, 1844.

Hyatt. Embryology of the Tetrabranchiates. (Bulletin, Mus. Comp. Zool. 1872).

Lankester. Development of the Cephalopoda. (Annals and Mag. Nat. Hist. 1873, and Quart. Journ. Micr. Sc. 1875).

Grenacher. Zur Entwickelungsgeschichte der Cephalopoden. (Siebold and Kölliker's Zeitschrift, 1874).

Ussow. Zoologico-Embryological Investigations. (Annals and Mag. Nat. Hist. 1875).

Consult also the writings of Van Beneden, Metschnikoff, D'Orbigny, G. & F. Sanberger, Barrande and Verrill.